PRIORITY EFFECTS AND ECOLOGICAL RESTORATION

Emanuela W. A. Weidlich[1,2*], Cara R. Nelson[3], John L. Maron[4], Ragan M. Callaway[4], Benjamin M. Delory[1], Vicky M. Temperton[1]

1. Ecosystem Functioning and Services, Institute of Ecology, Leuphana University, Lüneburg, Germany.
2. Present Address: Department of Botany, University of Santa Catarina (UFSC), Florianópolis, Brazil.
3. Department of Ecosystem and Conservation Sciences, Franke College of Forestry and Conservation, University of Montana, Missoula, USA.
4. Division of Biological Sciences and Institute on Ecosystems, University of Montana, Missoula, USA.

*Corresponding author: Emanuela Wehmuth Alves Weidlich. emanuela.ww@gmail.com

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Abstract

Priority effects refer to the order or timing of species arrival, including how species that arrive early to a site either positively or negatively affect establishment, growth, or reproduction of species that arrive later. Despite clear implications of priority effects on ecological restoration, to date there are no reviews of how and where priority effects have been studied and the extent to findings can be applied to restoration practice. Here, we survey the literature on priority effects and a) summarize patterns that are relevant to restoration; b) synthesize information on the mechanisms through which priority effects operate, and on how these mechanisms can be manipulated to achieve particular restoration goals; and c) highlight potential future research needed to improve use of priority effects in restoration. We found that even small delays in arrival time, as opposed to simultaneous arrival of species, can promote differences in subsequent community composition. Even so, there have been very few studies on the long-term stability of these priority effects, and the majority were conducted in temperate grasslands. Given the lack of information for other biomes, the general importance of priority effects, as well as its application to restoration, is unknown. Our findings suggest that creating alternative vegetation states via priority treatments might be a promising avenue to further explore, but that for the concept to be operationalized for restoration practice there is a need for research in the diverse types of ecosystems that are priorities for restoration and that occurs over longer time periods.

Keywords: Community assembly, competition, facilitation, historical contingency, plant order of arrival.

1. Introduction

Ecological restoration involves the reassembly of ecological communities after degradation. As such, theory related to community assembly and succession has the potential to improve restoration of degraded plant communities (Walker et al. 2007; Temperton et al. 2004; Young et al. 2017; Wilsey 2020). Historical contingency, that is the chance arrival of species after degradation, is key to community assembly and succession, but our understanding of contingency continues to emerge (Fukami 2015; Grman et al. 2013). We lack a generalized understanding of how contingency can not only influence restoration, but also how contingency can influence ecosystem structure and function.

Priority effects are important components of historical contingency, and refer to the order or timing of species arrival, or "who arrives when" (Fukami 2015). For example, priority effects include how species arriving early during assembly either positively or negatively affect subsequent plant establishment, growth, or reproduction (Vaughn & Young 2015; Temperton et al. 2016; Delory, Weidlich, von Gillhaussen, et al. 2019). Plant communities with the same species pool, but differing in species arrival order during assembly, may shift to alternative stable states, alternative transients states, or compositional cycles (Fukami 2015; Fukami & Nakajima 2011). These priority effects can have long-lasting effects on the structure and functioning of plant communities and thus have important implications for restoration efforts (Martin & Wilsey 2012; Wilsey et al. 2015; Weidlich et al. 2018).

The importance of order of arrival of different species in succession was originally discussed by Connell & Slatyer (1977), who postulated that the first colonists at a disturbed site may have positive (facilitative), negative (inhibition) or neutral (tolerant) effects on later species. Later, Quinn & Robinson (1987) coined the term "priority effect", focussing primarily on how early-arriving species suppressed later arrivals. Drake (1991) conducted, to our knowledge, the first experiment to test how species order of arrival affects final community composition. He found that the final species dominance patterns of bacteria and invertebrates were affected by the species that first arrived in the assembly sequence. Since then, studies reporting the importance of priority effects for the structure and functioning of ecological communities have proliferated (Ejrnæs et al. 2006; Körner et al. 2008; Grman & Suding 2010; Sarneel et al. 2016; Weidlich et al. 2018) .

In restoration, manipulating the order of arrival of plants, or groups of plants, can lead to communities that differ in structure and function, which together with other biotic and abiotic filters can help achieve desired plant communities (Hobbs & Norton 2004; Temperton et al. 2019). For example, in some systems it might be necessary to manipulate the identity of early-arriving species to promote positive interactions between early- and late-arriving species (e.g., Zwiener et al. 2014). Padilla & Pugnaire (2006) reviewed how such facilitation by early-arriving nurse species has been used in restoration of degraded lands. Understanding these patterns of variation and their drivers is critical for improving restoration outcomes. For instance, priority effects may not be evident in systems with strong equilibrium dynamics, but they might be important drivers of assembly in systems that easily shift into multiple alternative states (Chase 2003; Vannette & Fukami 2014; D'Antonio et al. 2017). Thus, strategies for using priority effect in restoration efforts are likely to be system-specific.

Restoration often involves manipulating which plant species are introduced, sown, planted, or transferred to a disturbed or degraded site at a given time (Weidlich et al. 2020). If the order of arrival of these species can affect ecosystem functioning or community composition over time, then priority effects can determine successful or unsuccessful restoration. This can be important for sustaining preferred species and resisting undesired species such as exotic invaders. Steering restored communities along particular temporal trajectories or towards particular ecosystem functions by using priority effects can be a powerful tool (Fig. 1). Examples in the literature include reducing invasive species (Lang et al. 2017; Stuble et al. 2016; Abraham et al. 2009), sustaining species that promote pollinator communities (Pocock et al. 2012), improving nutrient cycling, or increasing ecosystem productivity (Popp et al. 2017).

There have been thorough reviews of the mechanisms of historical contingency (Fukami 2015), community assembly and restoration (Young et al. 2001, 2005), and exotic invasions (Thomsen et al. 2011; D'Antonio et al. 2017; Hess et al. 2019). However, to date there are no summary reviews showing how and where priority effects have been studied (either native vs. native, or native vs. exotics). This information is needed to advance our basic understanding of priority effects in community assembly and to the practice of ecological restoration. Here, we survey the literature on priority effects and summarize patterns that are relevant to restoration. We then synthesize information on the mechanisms through which priority effects operate, with an eye towards how these mechanisms can be manipulated to achieve particular restoration goals. Finally, we highlight key gaps in the literature and suggest where future research is needed to better our understanding of how best to manipulate priority effects to advance restoration.

2. **Literature review**

We conducted a literature search in Web of Science using the following terms: "PRIORITY EFFECT" or "PRIORITY EFFECTS" and "PLANT*", refined into seven categories (Ecology, Plant Sciences, Evolutionary Biology, Forestry, Biodiversity Conservation, Environmental Science, Biology) and two document types (articles and reviews). Our survey addressed only English-language papers published until December 2019. We found 137 articles in our literature search, with the annual rate of studies increasing over time (Fig. 2a). From this total, 62 papers used the term priority effect only to interpret their findings, 42 articles experimentally tested priority effects (comparing simultaneous and non-simultaneous sowing/planting), and 18 papers investigated the role of early arriving species in the context of natural regeneration. Additionally, eight articles examined how evolutionary dynamics affect priority effects of early-arriving lineages (e.g., Wittmann & Fukami 2018) while seven papers evaluated sowing communities with different species richness, rather than manipulating order of arrival (Plückers et al. 2013; Carter & Blair 2012). Most of the studies tested or discussed priority effects with the motivation to apply results to management practices in restoration (Fig. 2b), indicating the applied relevance of priority effects.

3. General patterns from studies that tested priority effects

Priority effects can be asymmetric, contingent on environment and species composition, and persistent or not (Young et al. 2017), and in this context, 40 of the 42 studies that experimentally manipulated the order of arrival of different species found evidence for some sort of priority effect. For example, Sarneel *et al.* (2016) found that small differences in arrival time affected plant community assembly and diversity, both in the greenhouse and in the field. A number of experiments found that sowing legumes before other functional groups resulted in greater aboveground biomass production over time (Körner et al. 2008; von Gillhaussen et al. 2014; Weidlich et al. 2017) and lower total root length density and biomass in the upper layers of soil (Weidlich et al. 2018). The only two studies that found no evidence of priority effects when comparing simultaneous and non-simultaneous plantings were Mason et al. (2013) and Cleland et al. (2015).

Studies that experimentally manipulated the order of arrival of species were performed in four different biomes (Fig. 3a), but the 69% of experiments were in temperate grasslands. The over-representation of temperate ecosystems, particularly grasslands, was because most studies were in North America (62%) and Europe (33%), where around one third of the landscape is grasslands and grass-dominated landscapes. There were far fewer studies in tropical and subtropical wooded and grassland systems. Only 36% of the studies were performed in natural field communities, while most experiments were in greenhouses (49%) and outdoor common gardens with constructed communities (16%; Fig. 3b). Most experiments (57%) lasted less than one year (Fig. 3c). The time interval between the first and second sowing used in the non-simultaneous treatments in experiments testing priority effects varied from five days to three years (Fig.3d), but 43% lasted less than a month. Thus, our survey showed that even small delays in arrival time can promote differences in the community (as opposed to simultaneous sowings), but also that a large number of studies did not determine the stability of these effects. Studies that tested different sowing intervals found that a longer delay between sowings can create stronger priority effects (e.g., Young et al. 2017). They compared two experiments that delayed the arrival of exotic annual grasses for two weeks vs. one year and found that final native perennial cover was greater when the initial priority effect was allowed to establish for a longer time. von Gillhaussen et al. (2014) found that longer intervals between the first and second sowings of different functional groups led to experimental communities that were more productive.

Fifty-two percent of experiments compared priority effects between native and exotic species, while 48% tested interactions between native species (Fig. 3e). The studies testing the effects of an exotic arriving before or after a native species were mostly in North America (76%), whereas tests of natives vs. natives were more common in Europe (62%). In North America, South

America and Australasia, invasive exotic species strongly limited restoration success. Thus, the main goal of using priority effects derived from native species was to make communities more resistant to invasion (Funk et al. 2008). In contrast, invasive species were not as much of a problem for the restoration of European grasslands, and instead eutrophication and land use change were more serious restoration issues. Researchers in Europe tended to alter the order of arrival of different plant functional groups in order to study ecosystem functions (Weidlich et al. 2018), or to increase diversity and yield (Bullock et al. 2001, 2008).

4. Synthesis of general mechanisms driving priority effects and their relevance to restoration

Understanding the mechanisms that drive priority effects is essential. Fukami (2015) proposed that priority effects can be grouped into two broad processes; niche pre-emption and niche modification. In niche pre-emption the species that arrives first reduces the resources available to late-arriving species, resulting in inhibition. In niche modification, species “that have no or little overlap in their requirement components” either degrade or facilitate what other species require in their niches. These two processes can be divided into direct and indirect facilitation, and direct and indirect competition. Direct facilitative effects include providing shade, enhancing soil moisture through hydraulic lift, or increasing soil fertility, whereas indirect effects may be manifest through associational defences or changes in soil biota that favor other species (Callaway 2007). Direct competitive effects might include disproportionate resource uptake or allelopathy (Aschehoug et al. 2016), whereas indirect competition may occur through complex multispecies interactions (Levine et al. 2017), associational vulnerability to consumers (Barbosa et al. 2009) or changes in soil biota that suppress other species (Lekberg et al. 2018).

Combining both direct and indirect inhibitory mechanisms, Grman & Suding (2010) suggested that priority effects arise from asymmetric competition and soil legacies. Asymmetric competition occurs when interacting plants that differ in size create unbalanced competitive interactions, with the large plant having a much higher chance of outcompeting the smaller one. Soil legacies occur when the presence of a specific plant species affects the microbial community in ways that affecting the plant itself or other individuals of the same or different species. On the other hand, Gómez-Aparicio et al. (2004) tree seedlings planted under different nurse shrub species experienced both direct and indirect facilitation.

These inhibitory and facilitative processes that drive priority effects are difficult to use in restoration. This is because system-specific or species-specific information and in depth natural history expertise are often necessary, although trait-based assessments allow some generalization. For example, if preferred species are succulent they are highly likely to need nurse species (Valiente-Banuet et al. 2006; Romo-Campos et al. 2013), and the same is likely to be true for late-successional perennial species in general, such as in oak restoration (Callaway & D'Antonio 1991; Perea & Gil 2014). At a more geographic, or landscape scales, theory indicates that a need for facilitators might be more common in abiotically harsh conditions such as arid or alpine ecosystems (see Castro et al. 2004)). Padilla & Pugnaire (2006) noted that facilitation "has a practical side when applied to the restoration of degraded environments, particularly drylands, alpine, or other limiting habitats". Gómez-Aparicio et al. (2004) conducted a meta-analysis of experimental plantings of tree seedlings under different potential nurse shrubs species and found much stronger facilitation in a dry year than wet years, at drier and hotter low altitudes, and on sunny slopes than on shaded slopes. But facilitation can also promote restoration in many other systems. Evidence of facilitation in more moderate environments does suggest that its role may have been overlooked because of assumptions derived from the stress gradient hypothesis (Holmgren & Scheffer 2010; Temperton et al. 2007).

The judicious use of facilitative mechanisms may be advantageous early on in restoration, but priority effects caused by facilitation can also have a "dark side" (Lucero et al. 2019). Depending on the mechanism, exotic invasive species may be more strongly facilitated than natives (Maron & Connors 1996; Bulleri et al. 2008). Lucero et al. (2019) found that the highly invasive Eurasian annual grass, *Bromus rubens* occurred at far greater abundance under shrubs than away from shrubs in many sites across the Mojave and San Joaquin Deserts (USA). The very high density of *B. rubens* under shrubs correlated with very low abundances of native species. Desert shrubs commonly form "islands of fertility", and exotic invaders often benefit disproportionally from nutrient enrichment. Aschehoug & Callaway 2014) found that enriched soil fertility beneath *Quercus douglasii* trees shifted competitive advantages towards exotic annual species, to the virtual exclusion of native *Nassella pulchra*. Thus, nutrient enrichment as a facilitative priority effect should be carefully considered in restoration projects with a high potential for exotic invasions.

Nurse species can also have species-specific effects and mechanisms (Callaway 1998) that can be important in restoration. Gómez-Aparicio et al. (2004) compared the nurse effects of many different shrub species and found that legumes, small shrubs and spiny shrubs showed consistent positive effects on tree seedlings, but that rockroses had negative effects on seedlings. These results, in general, suggest that knowledge about the ecological traits, behaviour and natural history of species involved in facilitation in the restoration process is important.

The apparent suppression of natives by facilitated exotics (e.g., Lucero et al. 2019) illustrates how competitive priority effects may impede restoration (Dormann et al. 2000; Rinella et al. 2015). For example, in striking contrast to facilitative processes in shrub restoration in the semi-arid Mediterranean (Rinella et al. 2015; Gómez-Aparicio et al. 2004), Putz & Canham (1992) found that intense competition from several shrub species for soil resources and light created strong negative priority effects in disturbed north-eastern forests by retarding colonization by late successional tree species. However, competitive mechanisms varied with conditions; belowground competition was strongest in resource poor soil and competition for light more important at fertile sites.

Although competitive priority effects can impede succession and restoration outcomes in some cases, in others competitive priority effects could enhance restoration objectives by providing resistance to exotic invaders (D'Antonio & Meyerson 2002). A number of studies suggest that giving natives a head start may competitively resist invasion (Dickson et al. 2012; Cleland, Esch & Mckinney 2015; Ulrich & Perkins 2014). For example, (Delory, Weidlich, Kunz, et al. 2019) manipulated the timing of arrival of an exotic invasive species in Europe and the composition of the native community and found that inhibitory priority effects created by natives can decrease the risk of invasion by the exotic *Senecio inaequidens*. Stuble et al. (2016) varied the order of arrival of native and exotic species in a mesocosm experiment and found that both benefited from arriving early, but late arrival of exotic species affected their establishment less than that of late natives.

Competition among plants may be for resources, or through the release of harmful chemicals that negatively influence other species (Aschehoug et al. 2016). Allelopathy, or negative interactions mediated by chemistry, has been cited frequently as a mechanism promoting exotic invasion (Callaway & Ridenour 2004; Murrell et al. 2011), but whether allelopathic priority may frequently impede restoration is not clear. Lankau (2011) transplanted the late successional

Quercus rubra at eight different sites where the exotic *Alliaria petiolata* occurred. These sites varied in their invasion history and soil allelochemical concentrations. He found that native seedlings grew faster at sites with a longer history of invasion and lower allelochemical concentrations. He also found that the benefits of inoculating soil with native soil biota had stronger positive effects on the growth of the native species in newly invaded sites with more highly allelopathic invader populations. Lankau's results provide circumstantial evidence for allelopathy as a direct mechanism that can influence restoration, but the chemical effects of the exotic may be indirect, functioning through the suppression of mycorrhizae (Callaway et al. 2008), as suggested by the effects of soil biota inoculation in Lankau's research.

As for indirect facilitation, indirect competition is more difficult to detect or to use in predictable ways in a restoration context than direct competition. Priority effects involving indirect competition may occur when early-arriving species attract consumers that attack desired late-arriving species in restoration, or when they create strong plant-soil feedbacks that inhibit later species. Priority effects involving indirect competition may also occur when some species modify competition among other species (Metlen et al. 2013).

Restoration success often depends on indirect relationships with beneficial soil microbes that form symbiotic relationships with plant roots (Neuenkamp et al. 2019; Harris 2009). These relationships can change over time with reciprocal feedback effects of symbionts on plants and plants on symbionts. Such plant-soil feedbacks, which can involve the effects of soil biota as a whole, correspond with successional sequences of species (Kardol et al. 2006; van de Voorde et al. 2011), and thus are likely to affect restoration outcomes (Eviner & Hawkes 2008). We know of no experiments that have fully tested the *reciprocal* feedback process in the context of restoration (as opposed to succession), but tests of particular components suggest that the role of feedbacks in priority effects may be exceptionally strong. For example, Middleton & Bever (2012) experimented with early, mid, and late successional plant species planted near to or far from nurse plants that had received inoculation with native soil biota or not. They found negative effects of inoculation on early successional plants but positive effects of inoculation on mid to late successional plants, suggesting that feedback relationships in the context of restoration can contribute to priority effects that may be crucial to restoring late successional communities. Brinkman et al. (2017) found that conditioning degraded fen soil with plant species common in intact fen meadows produced more biomass of desired *Carex* species than when soils were conditioned with species from degraded fens. They proposed that growing typical fen meadow plant species in soil favored priority effects that improved the growth of other fen meadow species (also see (Larios & Suding 2014). In contrast, Yelenik & Levine (2011) found that plant-soil feedbacks did not match patterns of reestablishment of native plant species. They reported that climate and direct competition had stronger effects on native seedlings.

5. Knowledge gaps and future perspectives

***There is a need for large-scale and long-term experimental studies**:* Our review found a small number of field experimental studies (16 of 42) that lasted longer than a year (18 of 42). Considering that priority effects can vary over time (Werner et al. 2016; Weidlich et al. 2017) and space (Stuble et al. 2017; Young et al. 2017), there is a need to test the effects at restoration-relevant spatial and temporal scales because it is unclear how long priority effects relevant to restoration last. For example, an eight year field experiment (with a one year sowing interval) showed that priority effects lasted longer when grasses were sown before forbs than when forbs were sown before grasses (Werner et al. 2016). Thus, the persistence of priority effects across multiple generations and growing seasons deserves better investigation, and this can only be done with long-term studies that investigate how priority effects are mediated by environmental conditions (soil type, nutrient availability, climate change), and whether these effects last (Burkle & Belote 2015; Weidlich et al. 2017, 2018; Young et al. 2017).

***There is a need to evaluate other metrics of priority effects in addition to aboveground biomass**:* In experiments evaluating priority effects, aboveground biomass production was the most common variable measured (34% of studies; Supporting Information 1). We do not know if this is sufficient to clearly evaluate priority effects, or if measuring other parameters would lead to different results. For instance, (Körner et al. 2008) assessed aboveground and *belowground* shoot and root productivity in the context of priority effects, as did (Weidlich et al. 2018, 2017), Both Körner et al. (2008) and Weidlich et al. (2017, 2018) found that when legumes were sown first, plants invested less in roots and more in shoots, showing evidence of priority effects above and below the soil surface. These results beg the question of what are we missing by mainly measuring aboveground parameters?

***There is a need to study priority effect in restoration in different biomes**:* The large majority of studies on priority effects in our analysis were in temperate grasslands. Thus, more studies are needed in commonly restored habitats such as wetlands, forests, heathlands and savannas. Tropical and subtropical ecosystems, which harbour many of the global biodiversity hotspots and global commitments to landscape restoration (Brancalion et al. 2019), represented only 2.4% of the studies, with only one paper that tested the role of order of arrival in resistance to common invasive grass species (Evangelista et al. 2017). Plant order of arrival may have a different outcome in biomes with a variety of weather conditions and plant diversity. If the strength and direction of priority effects are sensitive to climate conditions during early establishment, it may affect how well different plants species manage to find adequate conditions to germinate and grow into adults. A few spatially and temporally replicated experiments have shown that the establishment of plants varied strongly between years and between sites (Stuble et al. 2017; Groves et al. 2020), showing that general patterns can be discerned, with higher dominance of in some years leading to different vegetation state (linked to temperature and precipitation). Thus, given the role priority effects can play in assembly is expected that weather conditions during the establishment can interact strongly with priority effects (Vaughn & Young 2010). Once we know how weather modulates priority effects (e.g. a hotter year leads to more grass establishment) during plant establishment, we can use it to manipulate assembly artificially aiming to favour restoration. Until studies are conducted in a wider variety of systems, understanding the general importance of priority effects is limited.

There is a need to study how priority effects determine multiple functions in landscapes and its feasibility for implementation in restoration: Manipulating order of arrival of plants can lead to alternative states in vegetation, which are important within the current context of aiming to achieve multifunctional landscapes in ecological restoration for biodiversity and climate mitigation. Increasingly, land management is being framed within a multifunctional landscape context, aiming for deriving multiple functions and services from different ecosystems (Manning et al. 2018). There may be instances where aiming for both restoring biodiversity as well as increasing productivity and carbon storage can go hand in hand, whereas in other cases stakeholders will need to agree on which key outcomes are the most important (Temperton et al. 2019). Creating alternative vegetation states via priority treatments might be a promising avenue for multifunctionality. For example, it might be possible to create priority effects that send landscape patches on particular trajectories (e.g., potentially high root productivity and soil organic C storage) by sowing grasses before other functional groups. In order to use priority effects within restoration to steer vegetation in desired directions, we need to fill several knowledge gaps. One clear need is for more field experiments to test the management strategies of priority effects in restoration contexts (Eriksson & Eriksson 1998; Grman & Suding 2010). In practice, would implementing a second sowing or planting be feasible given the extra expense involved? The gains of having non-simultaneous sowing or planting need to outweigh the costs in terms of time and input (e.g. more complicated sowing or planting regimes).

There is a need for trait-based predictions of priority effects in restoration*:* By focusing on functions in addition to taxonomy, trait-based approaches to biodiversity-ecosystem function research has better understood mechanisms underlying the effects of diversity. Since the success of traits-based approach to restoration is related to the diversity of the species involved, the strength of the environmental factors and on dispersal dynamics (Funk et al. 2008), integrating traits-based approaches to priority effects may also allow us to better understand mechanisms in restoration. For example, Funk et al. (2008) proposed to use suites of plant traits as surrogates with which to predict competitive resistance to invasion during restoration. They recommended selection of native species for restoration with traits similar to likely invaders. Beyond resistance to invasion resistance, Laughlin (2014) developed trait-based models that are useful not only for testing community assembly theories, but that also provide tools to achieve functional outcomes in ecological restoration. These models focus on which traits should be targeted according ecosystem stresses and restoration goals, and thus can be generalized to different systems. They suggested that ‘operationalising the response-and-effect traits framework (Suding et al. 2008) by translating functional traits targets into experimental species assemblages that can be manipulated by restoration practitioners’ is a way to achieve resilient and functioning ecosystems.

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Figure 1: Examples illustrating how priority effects might foster restoration within a plant functional group using or species approach. (a) The potentially strong facilitative role of legumes when they arrive before non-legumes. (b) A situation where one plant functional group was sown later than two others, for instance sowing a mixture of forbs and legumes first, and grasses arriving later, which might promote facilitation and allow deep rooting forbs species to establish before more shallow rooting grasses. (c) Priority effects caused by natives that resist against later arriving exotic invaders. (d) Species that grow fast and provide shade may supress invasive species, to the benefit of native species arriving later.

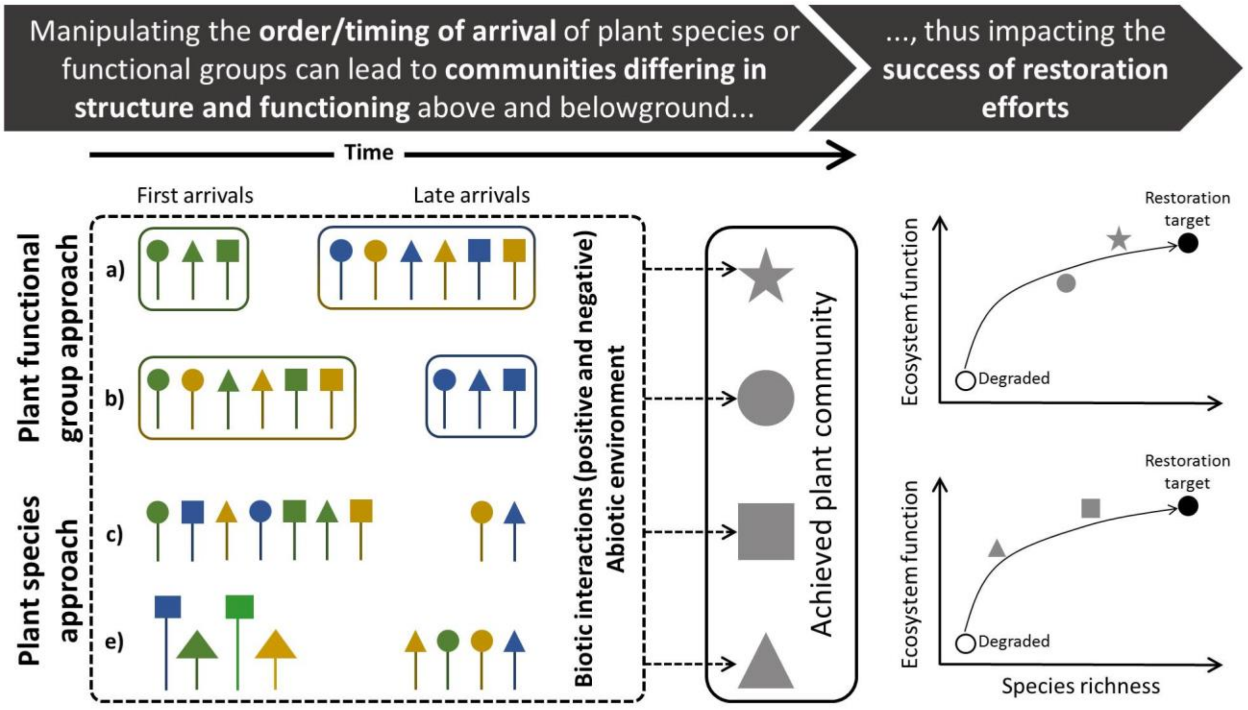

Figure 2: (A) Number of studies published per year on priority effects in plant communities. (B) Frequency of studies performed within a restoration context for each pool of papers. Among the 137 articles that mentioned plant priority effects, only 42 studies experimentally manipulated order/timing of arrival. The literature survey was made until December 2019.

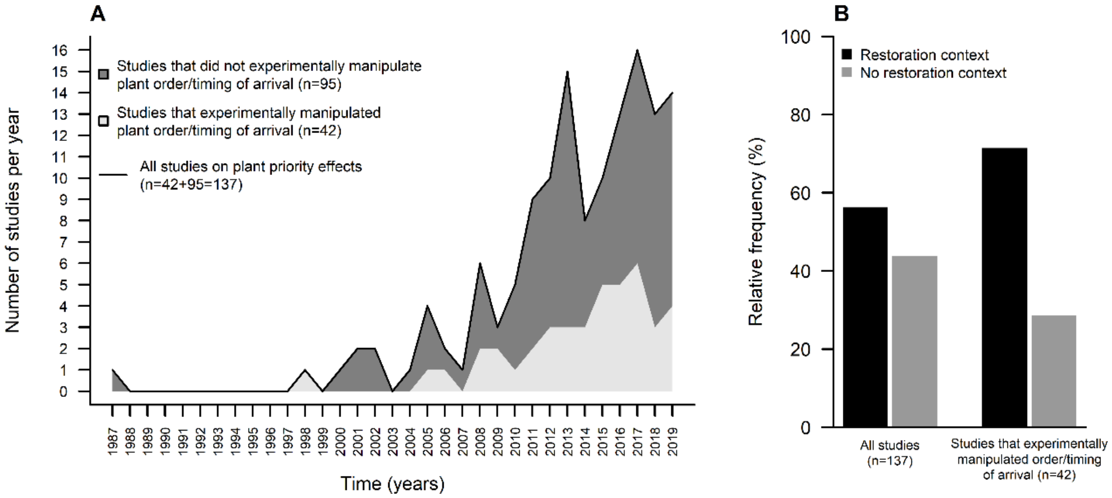

Figure 3: The majority of experiments that manipulated plant order/timing of arrival were performed in North America and Europe (A), in the greenhouse or in the field (B), and/or lasted less than a year (C). In the majority of these studies, priority effects were created using a sowing interval shorter than a month (D) and involved either natives only or natives and exotics (E).